FOLIAGE BIOMASS AND COVER RELATIONSHIPS BETWEEN TREE- AND SHRUB-DOMINATED COMMUNITIES IN PINYON-JUNIPER WOODLANDS

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ABSTRACT.—Woodlands dominated by singleleaf pinyon (*Pinus monophylla* Torr. and Frem.) and Utah juniper (*Juniperus osteosperma* [Torr.] Little) cover extensive areas in the Great Basin and Southwest. Both species are aggressive and can nearly eliminate the previous shrub-dominated community. Successional pathways from shrub-dominated communities before tree establishment to the tree-dominated communities that follow are known only for a few specific sites. How site growing conditions affect successional patterns needs further study. We compared the relationship of foliage biomass and percentage of cover between paired shrub-dominated and tree-dominated plots over several sites. Sites studied are from different elevation and topographic conditions on one mountain range. Foliage biomass in shrub-dominated plots had about a three-to-one variation over the range of site conditions sampled. Tree-dominated plots varied by about two to one. Cover in shrub-dominated plots had a four-to-one variation; cover in the tree-dominated plots varied by about two to one. Total foliage biomass in both tree- and shrub-dominated plots correlated best with the site index of height at 200 years of age. Variation in percentage of cover in both tree- and shrub-dominated plots correlated best with elevation. Foliage biomass variation in shrub-dominated plots was proportional to the variation in the paired tree-dominated plots. A similar proportional relationship was present for percentage of cover between paired tree- and shrub-dominated plots. Foliage biomass was more sensitive to topographic differences than to cover. Variation in plant species sampled in the shrub-dominated plots correlated with total foliage biomass of the same plots. Species sampled also correlated with pinyon height at 200 years of age and total foliage biomass in the paired tree-dominated plots.

Singleleaf pinyon (*Pinus monophylla* Torr. and Frem.) and Utah juniper (*Juniperus osteosperma* [Torr.] Little) woodlands cover more than 72,000 km² (18 million acres) in the Great Basin, coverage greater than it was before European settlement (Tausch et al. 1981). Both species are successionally aggressive and, once established, can nearly eliminate the understory. Loss of forage and increased soil erosion can result from dominance by the trees (Doughty 1987). Established woodlands provide wood products, pine nuts, and habitat for many wildlife species.

Successional pathways from shrub-dominated communities before tree establishment to the resulting tree-dominated communities that follow are known from only a few specific sites (Barney and Frischknecht 1974, Tausch et al. 1981, Young and Evans 1981, Everett and Ward 1984, Everett 1987). Variability in both tree- and shrub-dominated communities (Ronco 1987) complicates extrapolation of these results to sites of different growing conditions. Comparisons of biomass and cover relationships between shrub- and tree-dominated communities on the same sites are needed for more locations.

Woodlands have a higher percentage of cover at higher than at lower elevations and on north than on south aspects (West et al. 1978, Tueller et al. 1979). Both tree- and shrub-dominated communities appear to show an increase in cover, and in biomass, on the better sites. The potential three-dimensional form of these relationships is illustrated in Figure 1. Orientation of the X, Y, and Z axes in Figure 1 is for clarity of presentation of the three-dimensional representation.

The vertical X axis represents improving site conditions. Increasing cover or biomass in tree-dominated communities is represented by the Y axis. The Z axis represents increasing cover or biomass in shrub-dominated communities. The line a–e (Fig. 1) represents the relationship between site and shrub cover or biomass. The line a′–e′ represents the same relationship with site for biomass or cover of tree-dominated communities. If the relation-

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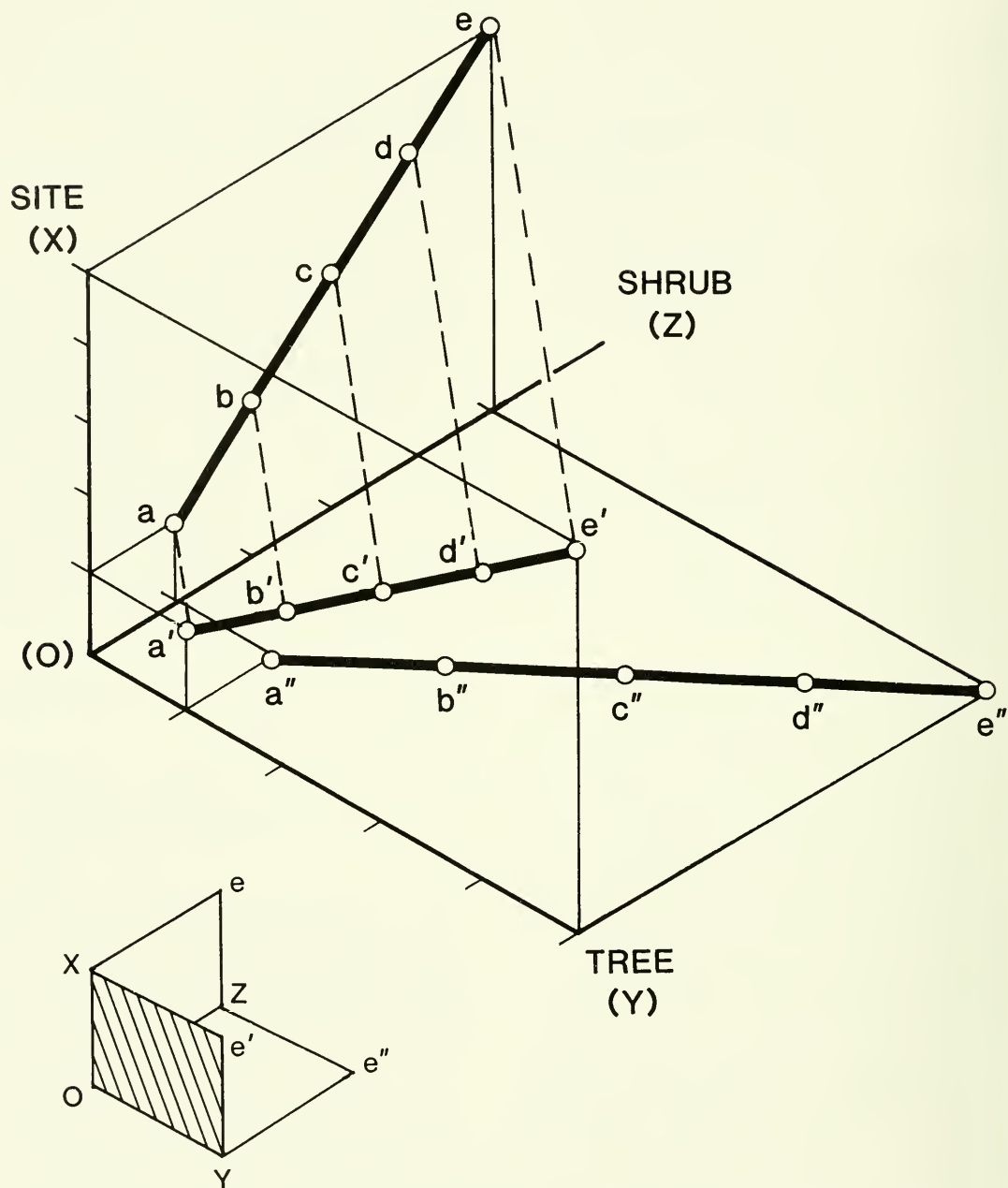[2]Department of Range, Wildlife, and Forestry, University of Nevada–Reno, Reno, Nevada 89512.

Fig. 1. Three-dimensional representation of hypothesized relationships between site quality (X) and cover or biomass in tree- (Y) or shrub-dominated (Z) communities in pinyon-juniper woodlands. The lines a–e, a'–e', and a"–e" represent hypothesized relationships among the respective axes.

ships of the X–Y and Y–Z planes hold true, a relationship also exists on the Y–Z plane. This is a proportional relationship between the quantities in the shrub- and tree-dominated communities represented by the a"–e" line.

The a–e–e'–a' plane (Fig. 1) represents the family of successional pathways for these communities for the site conditions represented. Succession in these woodlands without disturbance proceeds from shrub to tree domination

(Tausch et al. 1981). Dotted lines a–a' through e–e' estimate specific pathways for each site class. These pathways are drawn linearly only for visibility. They usually follow various types of curvilinear patterns (Tausch et al. 1981).

This study investigated the hypothesized three-dimensional relationship between cover or biomass of tree- and shrub-dominated communities and site. The X-Y, X-Z, and Y-Z planes in Figure 1 represent these relationships. Analyses used the total foliage biomass and total percentage of cover of tree-dominated and shrub-dominated communities of several sites on one mountain range. Sampled sites cover a range of elevational and topographic conditions.

Percentage of total vegetal cover has broad use in many other studies in these communities. Total foliage biomass (which can be directly related to leaf area) was included because it is a community dimension that reaches an equilibrium level in many forest types (Moller 1947, Marks and Borman 1972, Long and Turner 1975, Long and Smith 1984). More mesic sites than drier sites support higher equilibrium biomass (Waring et al. 1978). Equilibrium leaf biomass levels can be directly related to the hydrologic environment (Nemani and Running 1989). Other studies have also shown equilibrium levels of leaf biomass (or area) in relationship to site moisture conditions (Whittaker and Niering 1975, Grier and Running 1977) and nutrient stress (Waring et al. 1978). Only the endpoints of the potential sere on each site were sampled to increase the number of sites available.

METHODS

Data Collection

This study used six sites on the Sweetwater Mountains, Nevada and California (Table 1). We sampled a tree-dominated and a shrub-dominated plot at each site. The tree-dominated plots were fully stocked or fully tree-occupied as defined by Meeuwig and Cooper (1981). Shrub-dominated plots did not have trees larger than seedlings. These seedlings were less than 3 dm tall. Tree- and shrub-dominated plots were paired on each site on the same slope, aspect, and elevation. Plots were as close as physically possible while

TABLE 1. Aspect, slope, and elevation (m) for the six sample sites on the Sweetwater Mountains, Nevada and California. Plot identifications for tree-dominated plots from Meeuwig (1979) are in parentheses next to the site number.

Site	Aspect (degrees)	Slope (degrees)	Elevation (m)
1	81	3	2,120
2	75	2	2,030
3	90	4	2,280
4(S1)	80	3	2,210
5(S3)	120	9	2,300
6(S4)	345	20	2,020

still meeting the criteria for tree or shrub dominance.

TREE PLOT DATA.—Tree data for tree-dominated plots for three sites (4–6, Table 1) are from Meeuwig (1979) and Meeuwig and Budy (1979). We sampled additional tree-dominated plots on sites 1–3 (Table 1) to extend the elevational and topographic range of the data. All tree-dominated plots had only pinyon, except site 6, which had some juniper. Sites 2, 1, 4, and 5 represent a transect up the east side on the main alluvial fan and mountain slope of the Sweetwater Mountains. The sites cover the width of the woodland belt at about 100-m-elevation intervals. Site 3 is on the flat top of a foothill away from the main mountain mass, site 6 on a north-facing slope in a narrow canyon.

Tree-dominated plots for sites 1, 2, and 3 (Table 1) were 20×50 m in size (0.1 ha). We measured all trees in each plot for average crown diameter, tree height, and basal diameter about 15 cm above the ground surface. Where multiple trunks were present, we individually measured each trunk and determined a geometric average basal diameter (Meeuwig and Budy 1979). Tree foliage biomass and trunk cross sections were collected from a random sample of 12–14 trees in each plot (Tausch and Tueller 1988, 1989). These trees were aged by ring counts on two radii of their cross sections.

Tree-dominated plots for sites 4–6 from Meeuwig (1979) and Meeuwig and Budy (1979) were 30×30 m in size. All trees in each plot were measured using the methods described above and harvested. A random sample of the harvested trees was weighed to determine total wet and dry biomass for bole, bark, branch, twig, and foliage. Multi-

ple regression techniques were used to derive the total dry biomass values for each part and the total of the remaining trees on each plot from their measurements. Meeuwig and Budy (1979) aged all trees by ring counts. We extrapolated their leaf biomass data to a 0.1-ha plot size.

As a part of this study, we collected additional tree foliage biomass data from a random sample of trees adjacent to the plots from Meeuwig (1979) and Meeuwig and Budy (1979). These data were collected by the same techniques used for the tree-dominated plots on sites 1–3. Analysis results from these trees were used as an independent test of the foliage biomass predictions (Tausch and Tueller 1988).

SHRUB PLOT DATA.—Suitable shrub-dominated areas without mature trees varied in size between sites. Shrub-dominated plots on sites 1, 2, and 4 were 20 × 50 m (0.1 ha) in size. The largest shrub-dominated area on site 3 permitted a 15 × 30-m plot. Adjacent shrub-dominated areas of the same environmental conditions were not present for sites 5 and 6. A strong recovery by the understory was present in the plot areas originally cleared by Meeuwig (1979) and Meeuwig and Budy (1979) seven years earlier. Shrub-dominated plots 20 × 20 m in size were centered in their former tree plots.

We used five transects to sample plant species data on all shrub-dominated plots except site 3. These transects were 20 m long and randomly located perpendicular to the plot axis. Each transect contained 10 contiguous 1 × 2-m microplots, for a total of 50 microplots. Site 3 was sampled with seven randomly located transects 14 m long. Each transect was divided into seven 1 × 2-m microplots, for a total of 49 microplots. Although the overall plot size varied, the number of microplots sampled was equivalent for all the shrub-dominated plots.

The same techniques used in the 20 × 50-m shrub-dominated plots were used to collect understory data in the tree-dominated plots for sites 1, 2, and 3. Understory data were not available for the tree-dominated plots from Meeuwig (1979) and Meeuwig and Budy (1979).

We measured three crown dimensions on all shrub and perennial grass species in each microplot: (1) longest crown diameter, (2)

diameter perpendicular to the longest, and (3) height of the foliage-bearing portion of the crown. A random selection of the sampled microplots was used to collect foliage biomass for the more common measured species. Foliage biomass was collected from 24 random individuals of the dominant and co-dominant shrubs and 12 random individuals of the subdominant species in each plot. We collected foliage biomass of infrequently occurring species on both tree- and shrub-dominated plots whenever they were present in any microplot. All measured species in the understory samples of the tree-dominated plots, except the dominant shrubs, were sampled whenever present in a microplot.

We estimated the foliage biomass of forb and annual grass species in each microplot using the reference unit method (Andrew et al. 1979, 1981, Kirmse and Norton 1985, Cabaral and West 1986, Carpenter and West 1987). Actual foliage biomass of reference unit species was also collected in the random sample of microplots. This collected foliage biomass data provided a double sampling correction on the reference unit estimates. Foliage biomass of infrequently occurring forb species was collected whenever such species were present in any microplot. Percentage of each plot covered by each species of forb and annual grass was estimated for each microplot and averaged.

Data Analysis

TREE PLOT DATA.—We determined relationships of basal area to tree foliage biomass of the randomly sampled trees in each plot by nonlinear allometric regression analyses (Tausch and Tueller 1988, Tausch 1989). Analysis results were used to estimate the foliage biomass of the remaining trees in each plot from their basal diameters. Individual tree foliage biomass values were summed, for a total tree foliage biomass in each plot. The process was repeated for the trees sampled next to the three plots from Meeuwig (1979) and Meeuwig and Budy (1979). We used our tree data to predict their total foliage biomass values as a check on the methodology (Tausch and Tueller 1988).

Five indices of site class were used for this study: (1) Site Index I, height at an age of 200 years; (2) Site Index II, height at a basal diameter of 25.4 cm; (3) tallest tree, height of

the tallest tree on the plot; (4) average tree height, average height of dominant and co-dominant trees; (5) elevation, in meters of the sample site. Site Index I was determined by the techniques described by Aguirre-Bravo and Smith (1986). Their methods were successfully applied to pinyon in the New Mexico, Colorado, and Arizona area by Smith and Schuler (1988). This method uses the Chapman-Richards equation to fit the guide curve for a family of anamorphic site index curves. The equation is:

$$H = \theta_1 (1 - \exp(-\theta_2 A))^K \qquad (1)$$

where H = tree height, A = tree age, K = a constant equal to $1/(1 - \theta_3)$, and θ_1, θ_2, θ_3 = parameters of the Chapman-Richards equation. Equation 1 was fitted to the combined tree height and age data for all the sampled tree-dominated plots by an iterative, nonlinear regression procedure (Caceci and Cacheris 1984).

The average age and height of the dominant and co-dominant trees were based on the entire plot for sites 4–6. On sites 1–3 these averages were based on the randomly sampled trees that were dominant or co-dominant. We determined Site Index 1 for each tree-dominated plot, using these averages in a site-prediction equation based on equation 1 (Aguirre-Bravo and Smith 1986).

$$S = H \left[\frac{(1 - \exp(-\theta_2 A_0))}{(1 - \exp(-\theta_2 A))} \right]^k \qquad (2)$$

where A_0 = the age of reference (200 years), A = the average age of the dominant and co-dominant trees, H = the average height of the dominant and co-dominant trees, and S = Site Index I.

The second measure of site class, tree height at a constant basal diameter of 25.4 cm (Site Index II), was from work in Nevada pinyon-juniper woodlands by Chojnacky (1986). Nonlinear regression (Caceci and Cacheris 1984) was used to fit the allometric equation (height = a(diameter)^b) to the diameter and height data for all trees in each plot. We determined Site Index Class II height from the equation for each plot for the diameter of 25.4 cm. The last three site indices, average height of dominant and co-dominant trees, height of the tallest tree, and elevation, were used directly.

TABLE 2. Nonlinear regression results for basal area to foliage biomass relationships for trees sampled in tree-dominated areas of six sample sites. Data for sites 4, 5, and 6 are also discussed in Tausch and Tueller (1988). Site designations are from Table 1.

Site number	Sample size	r^2	Standard error (kg)
1	12	.97	3.15
2	12	.85	7.89
3	14	.98	1.03
4(S1)	12	.88	7.81
5(S2)	12	.92	3.93
6(S4)	12	.93	4.19

SHRUB PLOT DATA.—Crown volumes for the measured shrub species are based on the equation for one-half of an ellipsoid. A cylinder was used for the perennial grasses (Tausch 1980, Johnson et al. 1988). We used a sum of crown areas to compute percentage of cover of the measured species on each plot. Allometric equations were derived from crown volume and foliage biomass data randomly collected for each measured species, using nonlinear regression (Johnson et al. 1988, Tausch and Tueller 1988, Tausch 1989). These equations were used with crown volume data for the remaining plants in each plot to estimate foliage biomass by species.

Foliage biomass data from crown measurement and reference unit methods were summed for individual species total leaf biomass in each shrub-dominated plot. We extrapolated all data to a 0.1-ha plot size. Understory data from the tree-dominated plots on sites 1, 2, and 3 were similarly treated.

TREE/SHRUB/SITE COMPARISONS.—We used regression and correlation analyses to compare all relationships among total foliage biomass, total percentage of cover, and the five indices of site class. Total foliage biomass, cover, and the five site indices were also compared with the number of species sampled in the shrub-dominated plots.

A foliage biomass ratio (percentage) of the total in the tree-dominated plots divided by the total in the paired shrub-dominated plots was computed for each site. We computed a similar ratio (percentage) for total percentage cover. These ratios were compared with the number of species sampled in shrub-dominated plots and with the five site class indices by correlation analysis.

Table 3. Coefficient of determination values (r^2) for equations to predict ratio of crown volume to foliage biomass for the sampled shrub and perennial grass species. The letter *a* indicates plots where foliage biomass was collected from all individuals occurring in the sampled microplots. Site numbers are from Table 1.

| | Site number | | | | | | | | |
| | Shrub-dominated plots | | | | | | Tree-dominated | | |
Plant species	1	2	3	4	5	6	1	2	3
Artemisia tridentata vaseyana	.88		.81	.96	.95	.98	.91	a	a
A. tridentata wyomingensis		.87						.85	
Ceratoides lanata	.83			a	a				
Chrysothamnus vicidiflorus	a		a	.88	a				
Ephedra viridis					a		a		a
Eriogonum umbellatum				a	a				
Opuntia sp.				a					
Prunus andersonii	a			.96	.98		a		
Purshia tridentata	.99	.98	.96	.98	.78	.95	a	a	a
Ribes velutinum	.85			a	a		a		a
Symphoricarpos sp.									a
Elymus cinereus					.98				
Oryzopsis hymenoides			.87		a	a			
Poa sandbergii	.90		.81	.72	.95		a	a	a
Sitanion hystrix	.76	.86	.99	.81	.82	.86			
Stipa thurberiana	.87		.87	.86	a		a	a	

Table 4. Standard error of the estimate (g) for equations to predict ratio of crown volume to foliage biomass for the sampled shrub and perennial grass species. The letter *a* indicates plots where foliage biomass was collected from all individuals occurring in the sample microplots. Site numbers are from Table 1.

| | Site number | | | | | | | | |
| | Shrub-dominated plots | | | | | | Tree-dominated | | |
Plant species	1	2	3	4	5	6	1	2	3
Artemisia tridentata vaseyana	33.2		15.5	31.3	3.68	1.76	7.13	a	a
A. tridentata wyomingensis		1.79						1.60	
Ceratoides lanata	1.28			a	a				
Chrysothamnus vicidiflorus	a		a	3.64	a				
Ephedra viridis					a		a		a
Eriogonum umbellatum				a	a				
Opuntia sp.				a					
Prunus andersonii	a			1.70	.59		a		
Purshia tridentata	1.51	1.38	7.74	1.25	41.8	1.30	a	a	a
Ribes velutinum	46.6			a	a		a		a
Symphoricarpos sp.									a
Elymus cinereus					19.4				
Oryzopsis hymenoides			.07		a	a			
Poa sandbergii	.09		.07	.08	.03		a	a	a
Sitanion hystrix	.21	.18	.20	.06	.14	.18			
Stipa thurberiana	.29		.29	.06	a		a	a	

Relationships between the foliage biomass components of the shrub-dominated plots were determined by correlation analysis. The components used were the total shrub, total perennial grass, total cheatgrass, and total forb leaf biomass, and the number of species sampled. These five shrub-dominated plot components were similarly compared with the total foliage biomass in the tree- and shrub-dominated plots and with the five site indices.

Results and Discussion

Foliage Biomass Predictions

Tree data.—Prediction of pinyon total leaf biomass in Meeuwig's (1979) plots (4, 5, and 6, Table 1) using equations from trees we collected adjacent to those plots had an average error of +0.5% (Tausch and Tueller 1988). Equations for tree data on sites 1, 2, and 3 had coefficient of determination and standard error values very similar to those for sites 4, 5,
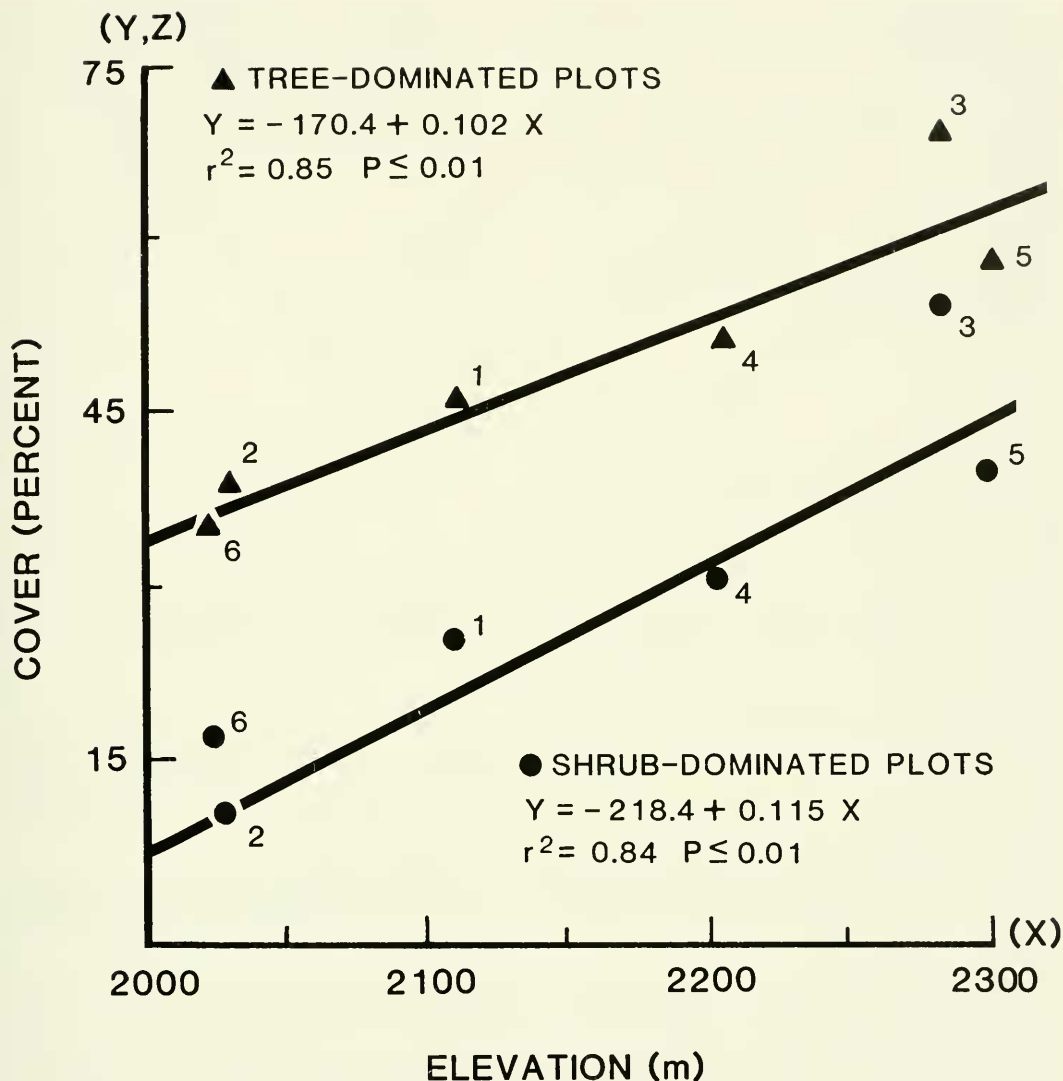
(Y,Z)

Fig. 2. Regression analyses between elevation and total percentage of cover in both tree-dominated plots and shrub-dominated plots. Axis designations follow those in Figure 1. Site numbers follow Table 1.

and 6 (Table 2). From these results we considered our tree data from sites 1, 2, and 3 to be similar enough to Meeuwig's (1979) tree data for sites 4, 5, and 6 for the data to be combined.

SHRUB, GRASS, AND FORB DATA.—Based on coefficient of determination (Table 3) and standard error of the estimate values (Table 4), prediction equations for the measured species have similar precision. Precision is also similar to the tree results (Table 2) and to other test results for sagebrush and bunchgrass foliage biomass (Tausch 1989). The mea-

sured shrub and perennial grass species averaged 98% of the total foliage biomass on the shrub-dominated plots. This combination also averaged more than 99% of the total foliage biomass of the understory in the three tree-dominated plots we sampled. Total understory foliage biomass on the tree-dominated plots averaged less than 0.50% of the total plot foliage biomass. We considered the error resulting from the lack of understory data for the three tree-dominated plots from Meeuwig (1979) and Meeuwig and Budy (1979) to be minimal.

Cheatgrass (*Bromus tectorum*) occurred on all sites and plots. Common forbs sampled included *Colinsia parviflora* and *Arabis holbolii* on all but site 2, and *Phlox longifolia* and *Descuriana pinnata* on all but sites 2 and 3. *Crepis accuminata*, *Lupinus caudatus*, *Lygodesmia spinosa*, and *Wyethia amplexicaulis* were present on sites 1, 4, and 5.

SITE CLASS INDEX.—The final Site Index I parameter estimates for the Chapman-Richards equation after minimizing the residual sum of squares were:

$$\theta_1 = 9.699$$
$$\theta_2 = 0.00764$$
$$K = 0.9342$$

Residual sum of squares = 281.1
Standard error of the estimate = 1.488
Coefficient of determination = 0.65

These parameters were used in equation 2 to determine the Site Index I value for each tree-dominated plot. They ranged from 6.48 to 9.69 m. Site Index II values (height at 25.4 cm basal diameter) ranged from 4.08 to 6.34 m. The heights of the tallest trees in the plots ranged from 6.9 to 11.1 m. Average heights of the dominant and co-dominant trees ranged from 4.6 to 8.8 m. The asymptotic height for the combined Sweetwater Mountains data (θ_1) is over 2 m higher than for the combined pinyon data for Arizona, Colorado, and New Mexico (7.63 m) from Smith and Schuler (1988).

Tree and Shrub Plot Comparisons

Total percentage cover in the tree-dominated and shrub-dominated plots for the six sites positively correlated with the elevation (Fig. 2). Figure 2 represents both the X–Y and X–Z planes in Figure 1. They also positively correlated with each other (Fig. 3). Figure 3 represents the Y–Z plane in Figure 1. Percentage of cover did not significantly correlate with any of the other four site indices based on tree height or with the total foliage biomass in the respective tree- or shrub-dominated plots. Percentage of cover on a total plot basis apparently does not clearly reflect leaf biomass.

Total foliage biomass in both the tree-dominated and shrub-dominated plots positively correlated with Site Index I (Fig. 4) and with each other (Fig. 5). Total tree leaf
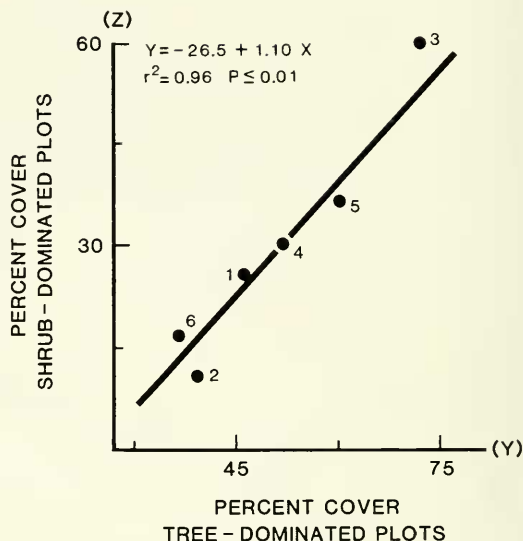

Fig. 3. Regression analysis between the total percentage of vegetal cover in tree-dominated plots and shrub-dominated plots over six sites. Axis designations follow those in Figure 1. Site numbers follow Table 1.

biomass and elevation were significantly correlated ($r = .83$, $P \leq .05$). Otherwise the total leaf biomass in tree- or shrub-dominated plots was not significantly related to the other four site indices.

The slope of the line in Figure 5 is deceptive because the ratio of tree to shrub foliage biomass was not constant between sites. This ratio was significantly negatively correlated with Site Class I (Fig. 6). Total foliage biomass in the shrub-dominated plots increased more with better site conditions (about threefold) than in the tree-dominated plots (about twofold). The slope in Figure 5 reflects both the actual ratio and its increase with higher levels of foliage biomass.

The lack of correlation between total foliage biomass and total percentage cover for tree- and shrub-dominated plots was not the case for individual species. Total foliage biomass of the two most common shrubs (mountain big sagebrush, *Artemisia tridentata vaseyana*, and bitterbrush, *Purshia tridentata*) had significant ($P \leq .01$) correlations ($r = .99$ and $r = .96$) with their respective percentage of cover values. Total foliage biomass of the most common bunchgrass (*Sitanion hystrix*) also significantly correlated ($r = .89$, $P \leq .025$) with its percentage of cover.
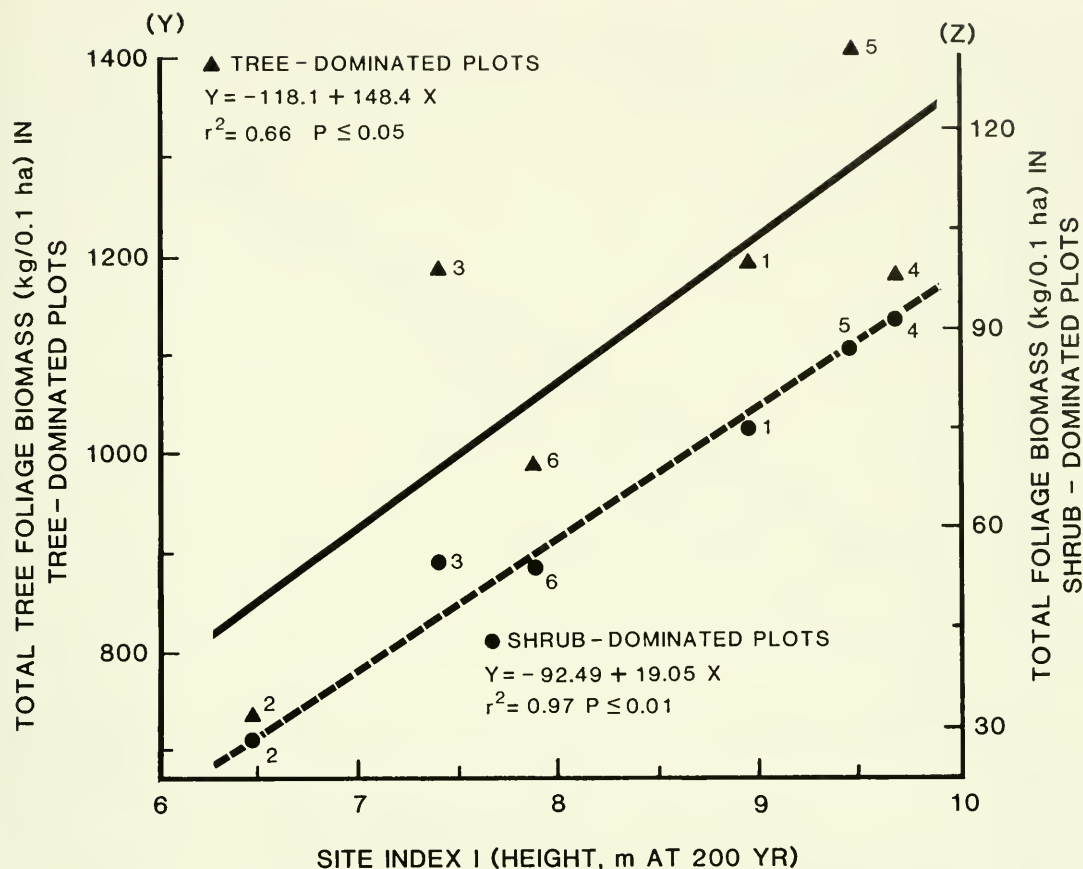
Fig. 4. Regression analyses between Site Index I and total foliage biomass in both tree-dominated plots and shrub-dominated plots. Axis designations follow those in Figure 1. Site numbers follow Table 1.

The number of species sampled in the shrub-dominated plots correlated with both the total foliage biomass in those plots and with Site Index I (Table 5). Species sampled also positively correlated with total foliage biomass of tree-dominated plots (Table 5) and negatively correlated with the foliage biomass ratio $(r = -.86, P \leq .05)$. But the species sampled were not significantly correlated with the vegetal cover in either the shrub- or tree-dominated plots, with the percentage of cover ratio, or with the other four site indices. A positive relationship occurred between the percentage of cover ratio and total tree foliage biomass $(r^2 = .81, P \leq .025)$, but not between it and the foliage biomass ratio.

Cheatgrass was negatively correlated with all the other components of the shrub-dominated plots (Table 5). The highest negative correlation for cheatgrass was with the total tree foliage biomass in the paired tree-dominated plots. Tree- and shrub-dominated plots had sufficiently similar environmental conditions for many relationships to exist between them.

A larger effect of topography on foliage biomass than on vegetal cover was evident in the data. Sites 2 and 6 were at nearly the same elevation and less than 200 m apart. Percentage of cover (Fig. 2) did not reflect the environmental differences between a steep north slope (site 6) and a flat alluvial fan surface (site 2). Topography strongly affected both tree and shrub plot foliage biomass data. Foliage biomass on the north slope (site 6) was about one-third more than on the fan (site 2). Differences in species composition may have also affected foliage biomass more than cover.

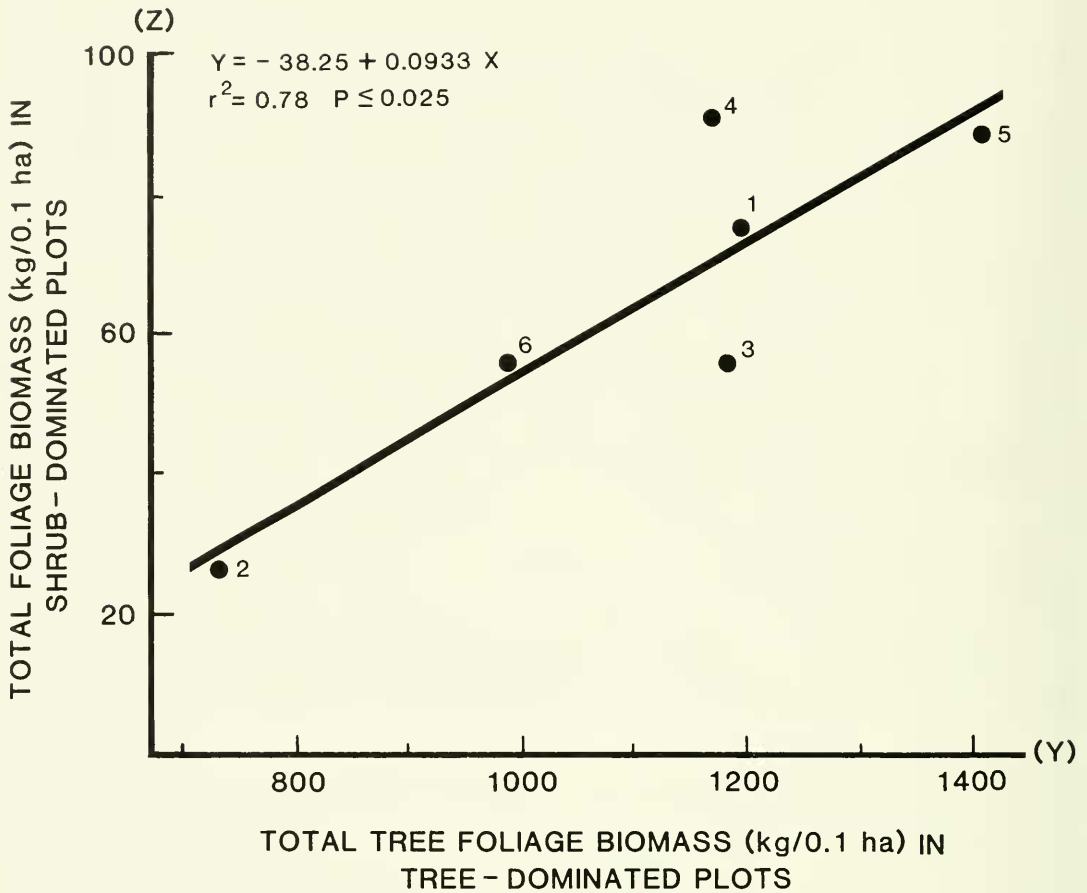Sites 3 and 5 are a similar comparison. Site 5, high on the side of the main mountain mass,

Fig. 5. Regression analysis between the total tree foliage biomass in tree-dominated plots and total foliage biomass in shrub-dominated plots over six sites. Axis designations follow those in Figure 1. Site numbers follow Table 1.

had jeffrey pine (*Pinus jeffreyi*) in the vicinity. Site 3, on top of a foothill, appeared drier but had slightly higher cover (Fig. 2). The higher cover on site 3 appeared to result from a higher density of smaller plants. For total foliage biomass, the situation was reversed, with site 5 about one-third higher than site 3.

The paired tree-dominated and shrub-dominated plots on each site were connected by dashed lines (Fig. 7) to approximate the a–e–e'–a' successional plane in Figure 1. The site-to-site connections between shrub- and tree-dominated plots were, with one exception, regular over the range of foliage biomass values sampled. At least on the mountain range sampled, the tradeoffs involved are generally consistent with the hypotheses of Figure 1.

Site Index I and elevation did not significantly correlate with each other or with the other three site indices. Site Index II, tallest tree, and average tree height were significantly correlated only with each other (Table 6).

CONCLUSIONS

Foliage biomass and percentage of cover variation in both shrub- and tree-dominated communities had significant responses to environmental differences. Responses reflected the hypotheses of Figure 1 but were not the same for foliage biomass or cover. Total foliage biomass in both tree- and shrub-dominated plots was correlated with Site Index I (height at 200 years of age). They also correlated with each other but not with percentage of cover. Percentage of cover correlated best with elevation. Total foliage biomass was more variable in response to topographic differences between sites than total percentage of cover.
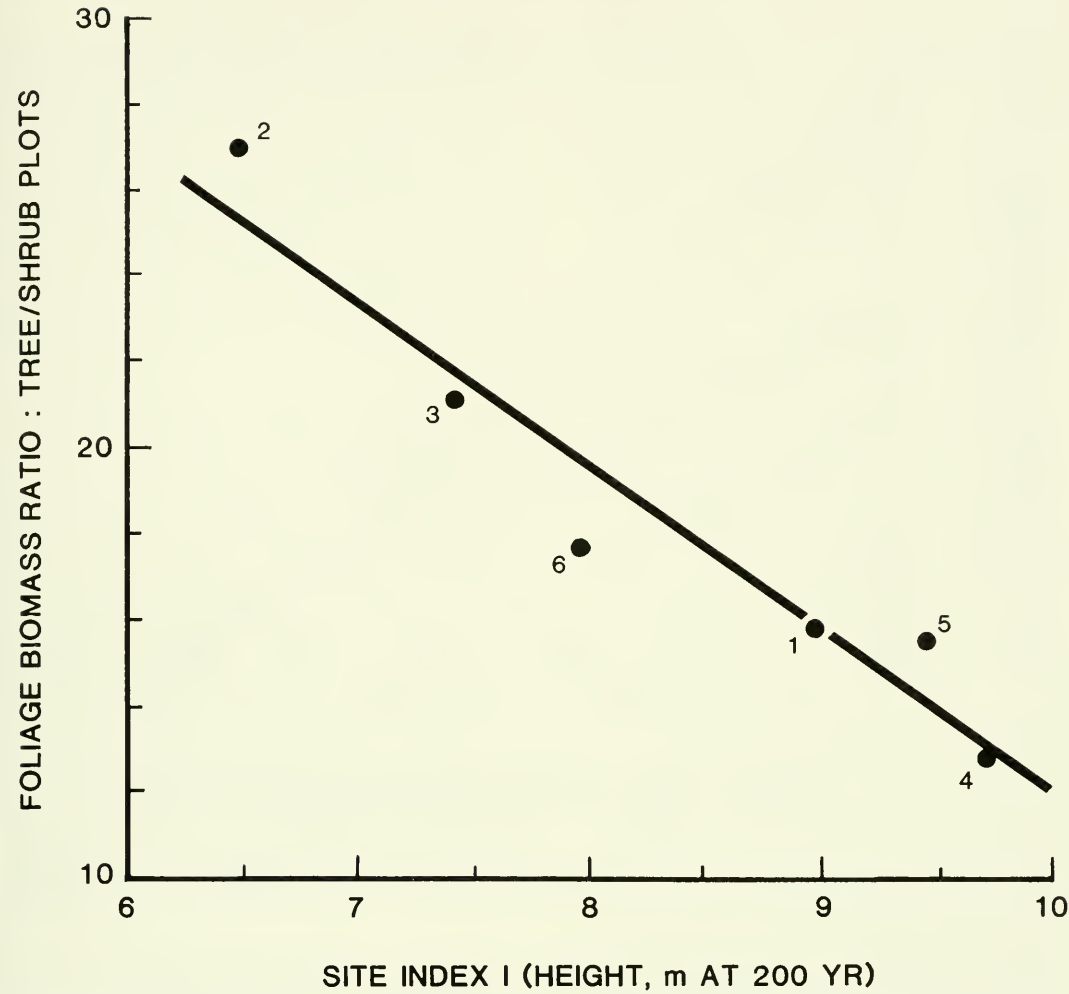
Fig. 6. Regression analysis between the Site Index I values and the ratio of total foliage biomass in tree-dominated plots divided by that in shrub-dominated plots. Site numbers follow Table 1.

TABLE 5. Correlation coefficients between four foliage biomass components and the number of plant species sampled in shrub-dominated plots, among those components and the total foliage biomass in tree- and shrub-dominated plots, and with Site Index I. Relationships between foliage biomass and Site Index I are in Figure 4.

	Total foliage biomass				Species sampled
	Shrub	Perennial grass	Cheatgrass	Forbs	
Shrub	1.00	.34	−.80[a]	.67	.82[b]
Perennial grass		1.00	−.51	.14	.76[a]
Cheatgrass			1.00	−.49	−.72
Forbs				1.00	.66
Species sampled					1.00
Total foliage biomass (tree-dominated plots)	.79[a]	.74[a]	−.87[a]	.28	.81[b]
Total foliage biomass (shrub-dominated plots)	.95[c]	.60	−.79[a]	.59	.94[c]
Site Index I	.92[c]	.60	−.71	.66	.96[c]

[a]$P \leq .10$.
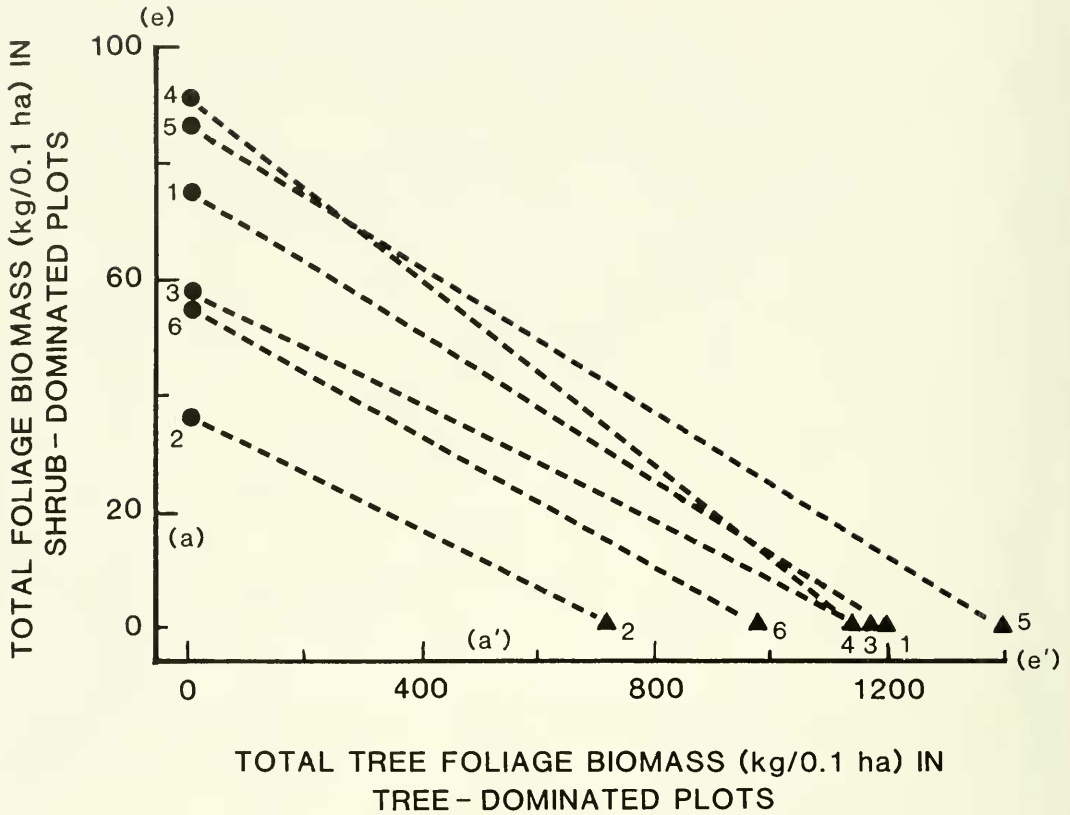[b]$P \leq .05$.
[c]$P \leq .01$

Fig. 7. Comparisons of the relationships between total foliage biomass of tree- and shrub-dominated plots on six sites on the Sweetwater Mountains. Axis designations follow those in Figure 1. Site numbers follow Table 1.

TABLE 6. Correlation coefficients among three site indices of tree height at 25.4 cm basal diameter (Site Index II), the height of the tallest tree, and the average height of dominant and co-dominant trees in six tree-dominated plots.

	Site Index II	Tallest tree	Average tree height
Site Index II	1.00	.97[b]	.91[a]
Tallest tree		1.00	.95[b]
Average tree height			1.00

[a]$P \le .05$.
[b]$P \le .01$.

Foliage biomass is also closely related to primary production (Whittaker and Niering 1975) and would appear to be a more sensitive measure for monitoring management results.

Foliage biomass and vegetal cover represented different indicators of environmental variation among sites. This appears to be related to the considerable size/density variation among individual plants and species possible when two or more sites are compared. A community of many small plants and/or many small species has higher vegetal cover than a community with the same total foliage biomass but with fewer, larger plants (Tausch 1980).

Foliage biomass on tree-dominated plots was about 12–25 times higher than on shrub-dominated plots (Fig. 6). This difference may be related to a more efficient use of site resources by the trees (Doughty 1987). Foliage biomass ratios also had inverse relationships to both total foliage biomass and increasing elevation. Total leaf biomass, and possibly annual productivity, in shrub-dominated communities increases more with better site conditions than in tree-dominated communities. The primary resource involved with improving site conditions appears to be moisture availability, as described by Nemani and Running (1989).

Our foliage biomass data for shrub- and tree-dominated communities are from only

six sites on one mountain range. They do not fully represent the range of variation present on that mountain range. In many areas of this and other mountain ranges the species composition of the tree- and shrub-dominated sites can have large variations from the sites used here. Specific foliage biomass levels and ratios could thus differ for other sites. Additional studies, particularly on a regional basis, will be needed to better establish the variation in the foliage biomass levels and ratios involved.

Height versus age curves, widely used in commercial forestry, appear to be useful in determining site class on Great Basin sites with pinyon, at least in the Sweetwater Mountains. For our data this site index most closely correlated with total foliage biomass and, therefore, potentially with primary production. A height versus age site index also appears to work equally well for both tree- and adjacent shrub-dominated communities on the same sites. An available index for site could potentially increase ease and accuracy of determining site potential for management of shrub-dominated communities, particularly in association with pinyon-juniper woodlands. Additional verification is required to determine the suitability of a site index method for this and other areas of the Great Basin.

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